THE ORIGIN OF PARASITISM IN BLOWFLIES

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As far as their larval feeding habits are concerned, the species of the family Calliphoridae (blowflies) can be divided into three groups: (1) obligate parasites, feeding on the tissues of living mammals and birds, and causing a condition known as myiasis in the host, (2) obligate saprophages, feeding on decomposing vertebrate carcases, and (3) a vast array of normally saprophagous species that can also act as facultative parasites. The question is whether parasitism or saprophagy is the primitive, ancestral habit. The question may be applied to the whole of the Cyclorrhapha.

Keilin (1915) noted that Cyclorrhapha larvae are very uniform in structure, but exhibit a very great diversity in life-habit, whereas Orthorrhapha larvae exhibit great structural diversity which is not accompanied by great biological diversity. Keilin asks how, then, can one explain the great diversity of Cyclorrhaphous larval habits coupled with such uniformity of structure? He concluded that the ancestral Cyclorrhaphan must have followed a life-habit from which the later great diversity was derived. He further concluded that this ancestral habit must have been parasitism. His reasons for holding this view are as follows:

1. A very large number of parasitic species are known among Diptera, but they are almost all Cyclorrhapha, not Orthorrhapha. Parasitism among the Orthorrhapha is extremely rare.
2. Larviparity and pupiparity, both adaptations to the parasitic habit, are again limited exclusively to the Cyclorrhapha and are absent from the Orthorrhapha.
3. Only in the Cyclorrhapha is there an enormous fauna of sarcophagous and myiasis-causing species. The latter may be considered to be a sort of transition between parasitic larvae with a long terminal saprophagous period, and truly saprophagous larvae.

Therefore, so Keilin argued, all free-living Cyclorrhaphous larvae are secondarily so, and the peculiar form of the free-living Cyclorrhaphous maggot is an example of the irreversibility of evolution.

Zumpt (1965) held the opposite view, believing that the parasitic habit in myiasis-causing species is derived from the free-living saprophagous habit. He saw the ancestral species of myiasis-causing flies as being very unspecialized feeders like the modern *Muscina stabulans* (Muscidae), which is saprophagous on dead vertebrates and insects, a scavenger in wasps' nests, a predator on other maggots and, occasionally, a myiasis agent.

He hypothesized that myiasis may have had two roots: a saprophagous and a sanguinivorous root. He saw the saprophagous root as beginning with species that bred in carcasses, which later became facultative parasites of suppurating wounds. This was then followed by a facultative parasitic habit on unwounded tissues, which eventually became an obligate parasitic habit. Zumpt saw intestinal parasites as arising from larvae accidentally swallowed in food.

The sanguinivorous root arose from larvae that preyed upon other maggots. Such larvae may have accidentally pierced the skin of a bird or mammal in its nest or burrow, thus obtaining a blood meal; these larvae would have evolved into obligate bloodsuckers. Zumpt, however, offered no evidence to support his hypotheses.

My own view, like Zumpt's, is that saprophagy was the ancestral habit, both among the Calliphoridae and the Cyclorrhapha as a whole. In response to Keilin's three points cited above, the following answers can be made.

1. While it is true that an enormous number of Cyclorrhapha are parasitic, it is also true that at least an equal, if not greater number are saprophagous. Parasitism, while not as common in the Orthorrhapha, is certainly not rare in that sub-order; the very large family Bombyliidae, and also the Nemestrinidae, Acroceridae and many Asilidae are parasitic as larvae.
2. The occurrence of larviparity and pupiparity in the Cyclorrhapha does not, in itself, indicate that the ancestral habit was parasitic.
3. Keilin's third point may be argued both ways; in other words the myiasis habit can easily be derived from the saprophagous habit, as shown by Zumpt.

Points in support of Zumpt's view are:

1. The parasitic habit among Cyclorrhapha is often linked with features that are obviously derived, e.g. the reduction of adult mouthparts and the absence of adult feeding in the Oestridae.
2. The widespread saprophagous habit among the Cyclorrhapha, even in many families that contain parasitic species, would indicate that this habit is primitive.
3. Parasitism is an all-embracing term that covers many different phenomena. For example, the parasitoid habit of Tachinidae is a very different phenomenon from the myiasis-causing habits of blowflies, and it is difficult to see how one habit could have arisen from the other. It is, however, easy to see how a generalized feeder like *Muscina stabulans* (see above) could have developed any one of the life-habits covered by the term 'parasitism'. It is very likely, therefore, that parasitism arose independently many times in the evolution of the Cyclorrhapha as a whole, and probably the Calliphoridae as well.

Regarding the peculiar form of the cyclorrhaphous larva, this appears to have evolved in response to the saprophagous habit, and does not indicate that the ancestral habit was parasitic. It simply shows that the 'maggot-form' is so successful that it enabled the Cyclorrhapha to invade a wide variety of habitats. In this paper, therefore, the hypothesis is that saprophagy is the plesiomorphic habit and parasitism the apomorphic.

The second question to answer is: What can the actual hosts of the Calliphoridae tell us about the evolution of the group? Although the Calliphoridae are known to parasitize many vertebrate and invertebrate groups, our concern in this paper will be restricted to the myiasis–parasitic habit in vertebrates. The vertebrates most commonly parasitized are without doubt the mammals, although birds and amphibians have a small number of highly specialized calliphorid parasites (Zumpt, 1965). It is interesting that there are very few records indeed of blowflies parasitizing reptiles, which seem to be the only class of land vertebrates that are effectively immune from attack. Zumpt (1965) cites a case of a gecko (*Naultinus elegans*) as a host of *Calliphora stygia* in Australia. Larval specimens sent to me from parasitized tortoises (*Testudo hermanni*) kept in captivity in Vienna, Austria, proved to be *Calliphora vicina* and *Lucilia ampullacea.*

Since the mammals are the main host group, what can blowfly parasitization patterns tell us about the evolution of blowfly parasitism? One of the most interesting points to emerge is that there are very few records of species of *Calliphora*, *Lucilia*, or *Chrysomya* parasitizing wild mammals in the wild state. All records known to me are either from zoo animals or animals in an urban situation. On the other hand, domestic mammals are frequently parasitized by these species. Even the obligate parasite *Chrysomya bezziana* has hardly ever been recorded from a wild mammal in the wild state, while it is recorded from 21 zoo mammal species from kangaroos (*Macropus rufa*) to Polar bears (*Thalarctos maritimus*) by Spradbery & Vanniasingham (1980). During many years of collecting, Zumpt (1965) never recorded *Ch. bezziana* from a wild African mammal, in spite of the abundance of this species in Africa.

What does this indicate? I suggest that these species may have evolved the parasitic habit in association with man. Further evidence in support of this view is that, of the six British species of *Calliphora*, the only two known to cause myiasis in any animal are the two synanthropic species *C. vicina* and *C. vomitoria*.

The endemic species of *Calliphora* in Australia include some, e.g. *C. augur* and *C. stygia*, that are known to be important agents of sheep myiasis (as well as breeding in carcases) yet none of these species has ever been recorded as a parasite of any indigenous marsupial, bat or dingo. This would suggest that the parasitic habit evolved after the arrival of man with his flocks of sheep to Australia, and that prior to this these flies must have bred exclusively in animal carcases. This seems to support strongly the view that parasitism in these species arose in association with man, and in response to the attraction of the unhygienic conditions prevailing in human dwellings and barns. It is possible that most blowflies do not parasitize wild mammals both because of their generally cleaner condition (in the wild) and because that niche has already been filled by the Oestridae and Gasterophilidae. It is also possible that domesticated breeds of livestock are genetically prone to blowfly attack, e.g. many varieties possess loose folds of skin or long, easily-soiled fleeces—features that are known to be attractive to blowflies.

If the above proposal is true it would probably follow that the parasitic habit evolved after man became settled in communities. It is quite possible, therefore, that archaeological evidence may shed light on this idea. It would be very interesting to make comparative studies of the insect faunas of archaeological sites that are known to have been heavily populated (by humans), and other sites that are known to have been only sparsely inhabited. This is a field in which both the entomologist and the archaeologist could make useful contributions.

References

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